

Indirect Effects of Predation in Human-Modified Landscapes

Ellinor Sahlén

Faculty of Forest Sciences

Department of Wildlife, Fish and Environmental Studies

Umeå

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Abstract

Large carnivores affect prey species, with cascading effects on entire ecosystems. In anthropogenic regions large carnivores come into conflicts with humans, especially in rural areas where farming and hunting traditions are widespread. As a result, large carnivores have been eradicated from many regions across their historical distribution. Here, I explore human-predator-prey interactions, and how large carnivores and humans affect the space use, behavior, and long-term stress of ungulate prey in a region greatly modified by humans. Experimental and observational data are used to quantify behavioral and physiological antipredator responses of prey in areas with and without large carnivores. Further, I synthesize the effects of large carnivores on ecosystems in anthropogenic landscapes, and outline implications of large carnivore recovery for extant prey species and humans.

I found that prey in my study areas responded to increased perceived predation risk, even where the focal carnivore species (brown bear *Ursus arctos*) had been absent for over a century. Prey selected more open habitats in areas where they perceived predation risk to be higher. Further, I noted that risk posed by brown bears had the potential to cascade across trophic levels and impact on tree recruitment.

Higher temperatures and human infrastructure were associated with higher hair cortisol (stress hormone) levels in moose *Alces alces*, which may have implications with respect to the globally rising temperatures and the increasing anthropogenic disturbances across many landscapes.

In anthropogenic regions, humans may greatly impact ungulates, predator-prey interactions, and the ensuing cascades. One way to mitigate human impacts is to preserve old-growth forests, because these tend to have lower human activity (less roads and no set rotation times) and cooler microclimates. Another important aspect is the mitigation of human-large carnivore conflicts, as human perceptions of large carnivores may be the most important factor determining the outcome of large carnivore recolonizations.

Keywords: *Alces alces*, antipredator behavior, browsing, cortisol, human-wildlife conflicts, large carnivores, long-term stress, predator-prey interactions, trophic cascades, ungulates

Author's address: Ellinor Sahlén, SLU, Department of Wildlife, Fish, and Environmental Studies, Skogsmarksgränd, 901 83 Umeå, Sweden
E-mail: ellinor.sahlen@gmail.com

Dedication

To my dad and my son; the past and the future. The wonders of nature were,
and always will be, best spent with you.

Hasta la vista, baby.

The Terminator

Contents

List of Publications	7
1 Introduction	9
1.1 Large carnivores and their impacts on ecosystems	9
1.2 Prey, predators, and people in anthropogenic regions	11
1.3 Objective	12
2 Materials and Methods	13
2.1 Study areas and model system	13
2.2 Study designs and data collection	14
2.2.1 Inducing risk—an experiment (Paper I)	14
2.2.2 Ungulate browsing patterns in bear country (Paper II)	15
2.2.3 Hair cortisol levels in prey (Paper III)	15
2.2.4 Ecological effects of large carnivores and implications of their recovery (Paper IV and V)	16
2.3 Data analyses and their rationale	16
2.4 Validation of stress hormone measures	17
3 Results and discussion	19
3.1 Antipredator behavior and cascading effects (Paper I and II)	19
3.2 Hair cortisol levels in prey (Paper III)	23
3.3 Ecological effects of large carnivores and implications of their recovery (Paper IV and V)	24
4 General discussion and implications for conservation	25
5 Conclusions	29
6 Perspectives for future research	31
7 Sammanfattning (In Swedish)	33
References	35
Acknowledgments	39

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Sahlén E., Noell S., DePerno C.S., Kindberg J., Spong G. and J. P. G. M. Cromsigt (2016). Phantoms of the forest: Legacy risk effects of a regionally extinct large carnivore. *Ecology and Evolution* 6(3), 791-799.
- II Sahlén E., Steyaert S., Kindberg J., DePerno C. S., Cromsigt J. P. G. M.*, and G. Spong*. Brown bears evoke a three-dimensional landscape of fear. (Manuscript)
- III Sahlén E., Cromsigt J. P. G. M., DePerno C. S., Kindberg J., and G. Spong. Large-scale spatial variation in long-term stress hormone levels in moose. (Manuscript)
- IV Kuijper D. P. J., Sahlén E., Elmhagen B., Chamaillé-Jammes S., Sand H., Lone K., and J. P. G. M. Cromsigt. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proceedings of the Royal Society B*. (In press)
- V Sahlén E., Cromsigt J. P. G. M., DePerno C. S., and G. Spong. The return of large carnivores amongst predator-naïve prey and people. (Manuscript)

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* These authors share senior authorship.

The contribution of Ellinor Sahlén to the papers included in this thesis was as follows:

- I Designed the experiment with co-authors, coordinated and conducted fieldwork, performed the statistical analyses, and wrote the main part of the manuscript.
- II Designed the study with co-authors, conducted fieldwork, carried out statistical analyses and wrote the manuscript.
- III Designed the study, conducted lab work, carried out statistical analyses, and wrote the manuscript.
- IV Organized the workshop of which the paper is based, coordinated initial outline, helped draft the manuscript, and created parts of the graphics.
- V Came up with the idea and wrote the manuscript.

1 Introduction

1.1 Large carnivores and their impacts on ecosystems

Large carnivores are known to affect biodiversity and ecosystem function, thereby greatly impacting the environments they occupy (Ripple *et al.*, 2014). They affect prey species abundances, behaviors and physiology, but also other species through indirect and cascading impacts across trophic levels (Creel *et al.*, 2007; Berger *et al.*, 2001a; Lima, 1998). The last two decades, an increasing amount of research has been devoted to investigate how, when, and where large carnivores affect lower trophic levels (Ripple *et al.*, 2014; Mech, 2012).

Carnivores may affect prey species directly (predation) and indirectly (behavior). When carnivores hunt to feed—they kill, which leads to a reduction in prey population size as prey individuals are eliminated. The direct effects of predation can therefore greatly limit prey populations, especially if it leads to additive mortality for the prey species (i.e., not only non-reproductive or young individuals are targeted). However, due to the strong selection of predators on their prey, prey species have evolved traits—behavioral, morphological, and physiological—to avoid predation (Kats & Dill, 1998; Lima, 1998). For example, in the presence of predators, prey are likely to be more cautious, or vigilant, to reduce the risk of being killed (Brown *et al.*, 1999). Ungulates may spend more time scanning their surroundings while foraging in areas where risk is perceived to be higher, or use their senses of smell and hearing to detect large carnivore cues (Lima, 1987). However, how ungulates respond to risks depends on many other factors such as individual health status and dependent young (Poole *et al.*, 2007; White & Berger, 2001), predator hunting mode (Lone *et al.*, 2014; Preisser *et al.*, 2007), habitat characteristics (Kunkel & Pletscher, 2000), and previous risk regime (Sih & McCarthy, 2002), amongst others. Antipredator responses have associated costs (missed opportunities to

forage or reproduce), which may compromise lifetime reproductive success and survival (Sih *et al.*, 2010). If predators disappear from a system, prey species may lose their evolved antipredator behavior over time and become 'naive' to the predator (Berger *et al.*, 2001b). These processes are important to investigate if large carnivores are expected to return to previously occupied areas.

Predation risk is not uniform across the landscape, as there are certain habitat types where prey are more likely to be killed or encounter predators (Laundré *et al.*, 2010). Laundré *et al.* (2001) describe this as prey living in a landscape of fear. Ungulates and other prey use landscape structure, vegetation and terrain, along with their senses, to avoid dangerous situations in places where risk is perceived imminent or increased (Kuijper *et al.*, 2013; Ordiz *et al.*, 2011). Landscapes of fear may contain contrasting risks (Atwood *et al.*, 2007), especially in areas where prey is exposed to several predator species occurring across the landscape with different habitat preferences or hunting modes (e.g., cursorial, opportunistic, or ambush). Specifically, in human-modified landscapes, humans may create a risk landscape that contrasts to that of other predators in the system (Lone *et al.*, 2014). Thus, prey species living in areas greatly affected by humans may have to deal with contrasting or synergistic risks, which impact prey behavior and their stress load. Many studies have evaluated the impact of risk across landscapes in terms of behavioral responses in ungulate prey; however, physiological stress responses to predation risk and other landscape characteristics extrapolated on a landscape scale (investigated in Paper III) are largely unknown (Bourbonnais *et al.*, 2013), but may be useful to understand species interactions and anthropogenic effects on species dynamics.

Predation rates and the indirect consequences of predation (also called non-consumptive effects or trait-mediated effects) may be important in shaping prey population dynamics and cascading effects on lower trophic levels (Creel & Christianson, 2008; Preisser *et al.*, 2005). Top-down cascading effects of large carnivores generally occur along two main paths; through changes in prey species abundances (density mediated) and through changes in prey behavior (trait mediated) (Schmitz *et al.*, 2000). Density-mediated trophic cascades have been discussed in the literature for some decades (Isle Royal, McLaren & Peterson 1994), but during the last decade or so, there is increasing evidence for behaviorally mediated trophic cascades for large mammal systems (Kuijper *et al.*, 2013; Schmitz *et al.*, 1997). By reducing ungulate numbers and affecting where ungulates forage, large carnivores can release vegetation from suppressed states (so called browse traps) (Staver & Bond, 2014), but also affect nutrient deposition and trampling impacts on vegetation. Most studies

about terrestrial trophic cascades come from North America, and North American national parks in particular (Mech, 2012), whereas few studies have looked at the potential for large carnivore-induced trophic cascades in landscapes heavily modified by humans—particularly in Europe, where large carnivores are currently recolonizing new grounds. In Papers I and II, I am exploring behavioral responses of prey to large carnivores and potential cascading effects on plant recruitment in human-modified landscapes. Such knowledge is important to successfully manage complete multi-species systems, which is considered the way forward in modern adaptive natural resource management.

1.2 Prey, predators, and people in anthropogenic regions

Notably, humans affect species abundance and landscape configuration, directly and indirectly affecting most trophic interactions in some way, may it be through hunting, forestry, or e.g. nutrient deposition. Therefore, human actions influence the ecological roles of large carnivores by affecting their density and behavior, and those of mesopredators and prey species; processes I explore in depth in Paper IV.

In addition, it is becoming increasingly clear that our land use alterations and emissions of greenhouse gases affect wildlife species by globally warming temperatures. The consequences for different species depend on their specific adaptations to their environments—morphological and physiological—, and their ability to quickly adjust to new situations (Hoffmann & Sgro, 2011). For example, on the northern hemisphere mismatch in camouflage for species dependent on coat coloration (e.g., snow-shoe hare *Lepus americanus* or Arctic fox *Vulpes lagopus*) may dramatically impact their performance if they are unable to quickly adjust to unpredictable snow or absence of snow (Zimova *et al.*, 2016).

Within all these human activities there are stakeholders, which makes wildlife management complex and some conservation efforts challenging. As human interests are wide-ranging, and even expand into areas where humans themselves are rare, large carnivores and humans often compete at the apex position of ecosystems (Gangaas *et al.*, 2013). As a result, large carnivore populations have been persecuted and eradicated from much of their native ranges over the last couple of centuries, to make room for human activities and infrastructure. Thus, the main conservation threats towards large carnivores are habitat loss and massive human-wildlife conflicts due to predation on livestock and prey (game) species, which generally generate negative attitudes against large carnivores (Ripple *et al.*, 2014). Research has shown that negative

attitudes and conflicts with large carnivores are more widespread in areas where these disappeared and then recolonized (Gangaas *et al.*, 2013). Therefore, in the light of the large carnivore comeback now seen in Europe and on other continents, the effects of predators on prey are likely more important now than ever. Especially in human-modified landscapes, where prey and humans may be relatively inexperienced with large carnivores (Paper V), more knowledge about the impacts of large carnivores on ecosystems will facilitate large carnivore recovery, as people in affected areas can get more accurate information about the potential costs the return of large carnivores might carry.

1.3 Objective

With this thesis, my aim is to expand the existing knowledge base of antipredator behavior and its ecological effects, which can be used to guide future research and management in areas where large carnivores exist or are recovering. With various methods, I investigate the effects of predators (including humans) on trophic and behavioral processes in anthropogenic landscapes. I attempt to give insight into the complex processes that may transpire when once exterminated large carnivore populations are let to recover in areas dominated by humans.

Specific objectives were to:

1. Experimentally investigate the presence and nature of antipredator response in predator-inexperienced ungulates by determining ungulate visitation to different risk treatments in a human-modified landscape (Paper I)
2. Document antipredator behavioral trade-offs in predator-experienced ungulates by quantifying browsing and potential impacts on vegetation (Paper II)
3. Investigate the relative effects of external stressors, including predator occurrence and humans, on hair cortisol levels in moose (Paper III)
4. Synthesize the effects of large carnivores on ecosystems in anthropogenic landscapes, and develop research agendas (Paper IV)
5. Outline implications of large carnivore recovery for extant prey species and humans (Paper V)

2 Materials and Methods

2.1 Study areas and model system

Scandinavia holds biomes ranging from arctic tundra in the north to temperal broad-leaved forests in the south, with the majority of the country constituted of boreal forests dominated by Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. Several large carnivore and ungulate species occur, but not in all regions, which makes Sweden a suitable location to study species- and trophic interactions.

The study areas for Paper I and II (Figure 1) are both situated in landscapes altered by humans. One is dominated by extensive forestry and agriculture (Paper I) and holds several ungulate species (roe deer *Capreolus capreolus*, fallow deer *Dama dama*, moose *Alces alces*, red deer *Cervus elaphus*, and wild boar *Sus scrofa*), but no or very few large carnivores (sporadically occurring lynx *Lynx lynx*), whereas the other is dominated mainly by industrial forest and situated in one of Sweden's most densely populated brown bear *Ursus arctos* areas (0.3 bears/10 km², Solberg *et al.* (2006)). Our study areas had no or very few wolves *Canis lupus*, and in the latter study area predation on moose (and roe deer) was predominately caused by brown bear (Swenson *et al.*, 2007). Brown bears have been shown to have strong limiting effects on ungulate species, especially by the killing of fawns or calves during summer (Swenson *et al.*, 2007; Zager & Beecham, 2006). Thus, use of habitat preferred by brown bear is likely to increase risk for ungulates (females and calves in particular), especially as brown bears hunt in an opportunistic manner (Bastille-Rousseau *et al.*, 2011).

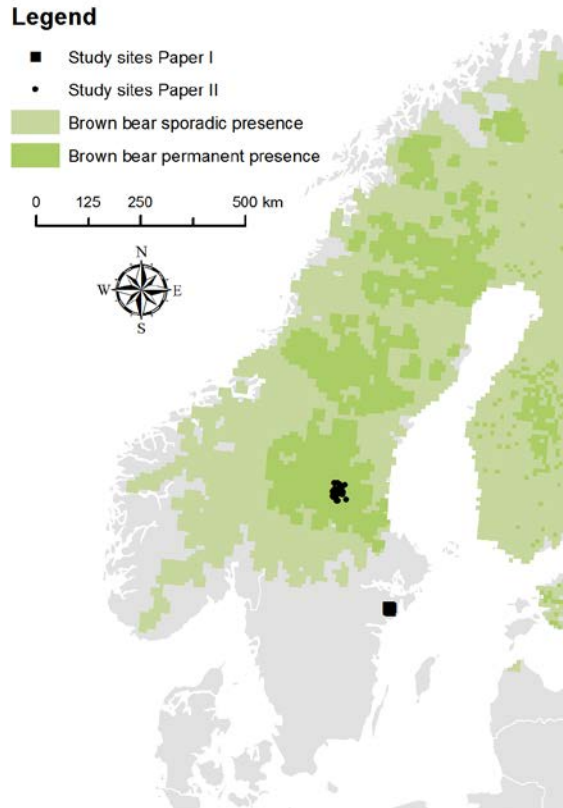


Figure 1. Location of study areas. Brown bear distribution is based on Chapron *et al.* (2014).

2.2 Study designs and data collection

2.2.1 Inducing risk—an experiment (Paper I)

I introduced pieces of brown bear pelt (scent) to 30 feeding sites in our southern study area, located to the southeast of current brown bear range (Figure 1), to investigate the responses of several species of ungulates to a regionally exterminated large carnivore. Ungulates at each site were exposed to brown bear pelt, and to pelt from reindeer *Rangifer tarandus*, a non-carnivore species not occurring in the study area, for a week. In addition, ungulates were exposed to a control treatment without scent, also for a week. Thus, each site had three treatments in a specific order, and the orders at sites were exactly balanced throughout the experiment to account for potential lingering effects

(e.g., in the case brown bear scent had lasting effects influencing the following treatment). Horizontal cover was quantified using sighting distance, which was measured by walking away from a sighting distance device until it was completely hidden in four cardinal directions. Cameras were mounted at the site at chest height to record visitation, and I assessed visitation (the amount of times the camera detected the presence of ungulates) for each ungulate species and site.

2.2.2 Ungulate browsing patterns in bear country (Paper II)

Based on a brown bear resource selection function map from the Scandinavian brown bear research project, I divided bear habitat selection data into three classes, and study sites were distributed in the lowest and highest levels of bear use (10 in low, 11 in high) to ascertain spread and contrasts in risk levels. I distributed 20 plots within each site, where I quantified browsing in different height classes and documented the height of the tallest sapling to measure tree recruitment. I measured sighting distance (as specified for Paper I), counted potential escape impediments and assessed habitat type. Further, for every plot, selection ratios for each height class were calculated. I measured distance to the nearest road (using a geographical software) and used cumulative primary productivity measurements at the location of each plot to control for the effects of roads and productivity on browsing and tree recruitment in plots.

2.2.3 Hair cortisol levels in prey (Paper III)

I asked hunters across Sweden to collect hair samples from moose shot during the moose hunt in fall 2012. Samples were collected by cutting the hair as close to the skin as possible over an area of approximately 4 cm². Hunters documented the GPS-location of the kill site, general health status and older injuries of the moose, demographic group (male/female/calf), and the hunting method by which it was killed. A total of 389 samples were received by mail to our laboratory. Hair samples were prepared and analyzed with an enzyme-linked immunoassay to quantify cortisol concentration. Explanatory variables used in statistical analyses are explained in detail in Paper III, but were related to; human activity, ungulate density, temperature, carnivore density, and moose demographic group.

2.2.4 Ecological effects of large carnivores and implications of their recovery (Paper IV and V)

For paper IV, we synthesized the existing knowledge about the ecological effects of large carnivores in human-modified landscapes, and developed agendas for future research. We assessed the geographic origin of studies investigating trophic cascades and constructed a conceptual overview of how humans may affect trophic cascades. For Paper V, I reviewed literature to explore how the return of large carnivores to anthropogenic landscapes may affect prey species and humans, and highlight implications for large carnivore conservation.

2.3 Data analyses and their rationale

Due to repeated measurements on several unit levels (in my case spatial pseudoreplication across plots and sites) I used generalized linear mixed effect models (GLMMs) in Paper I and II to analyze the data, as these models allow both fixed and random effects to be specified and taken into account in the analysis. Both count data and proportion data was overdispersed (there was more variability in the data than expected in the assumed distribution) and I used quasi-poisson and quasi-binomial errors to account for this. Unfortunately, Akaike's information criterion (AIC, penalized log-likelihood) is not defined for these types of models, so instead I used stepwise model simplification by removing insignificant terms (alpha level 0.05).

When analyzing hair cortisol levels (Paper III) I used generalized linear mixed models and multi-model inference using AIC (however, ANOVAs were used in the analytical validation of cortisol as a potential biomarker of long-term stress (see section 2.4)). Explicitly, AIC penalizes parameters that are redundant in a model, which makes it a good criterion for model selection procedures. First, I created a priori model sets by categorizing parameters that I predicted to be ecologically relevant for moose. Variables that were included in any of the category top model sets within a cut-off value of $\Delta AICc < 2$ were carried forward into a comprehensive model of variables influencing hair cortisol levels in moose. I checked for multicollinearity between variables (Pearson's and variable inflation factors [VIFs]), and excluded correlated variables. Throughout all statistical analyses, I generally limited myself to include two-way interactions, as three-way interactions often are hard to interpret.

2.4 Validation of stress hormone measures

The validation of an immunoassay (which measures the presence or concentration of a molecule in a solution through the use of an antibody) is based on two main validation steps: analytical validation and biological validation. The analytical validation demonstrates that the target hormone is precisely being measured and commonly consists of determining cross-reactions with other hormones, precision (repeatability), parallelism between standards and unknowns, and the minimum detectable quantity of the target hormone, amongst others (Paper III).

Whereas analytical validation is relatively easily conducted in the environment of a laboratory, biological validation is generally more challenging. Biological validation should demonstrate that the hormonal measures actually reflect the physiological status of the sampled individual. More specifically for cortisol (stress hormone), this means the cortisol measured should reflect the overall stress load for that individual. If measuring cortisol in blood or feces, a pharmaceutical challenge test of the hormonal response can relatively easily be done (with ethical permission). Commonly, ACTH (Adrenocorticotrophic hormone), which stimulates the production and release of cortisol to the blood stream, is administered, with a predicted following rise in systemic cortisol level. This rise is then monitored and reflected in blood or feces samples after some time (a few minutes in blood and a few hours to days in feces, depending on species). For hair cortisol studies, this part is commonly difficult to carry out, partly because hair incorporates cortisol gradually and slowly, which would demand several pharmaceutical challenge tests on individuals with regular intervals for a long period of time. Because of these difficulties (along with the assumption that cortisol in hair properly reflects the systemic cortisol exposure in the body), studies sometimes do not report physiological validations at all and therefore the biological reliability is poor. For ungulates, a rise in hair cortisol levels following administrations of ACTH was successfully shown for dairy cattle (Gonzales-de-la-vara *et al.* 2011), which most likely also correspond to other large ungulate species.

However, biological validation has also been carried out in ways where hair cortisol was determined after a long-term stressful event. For example, translocation of captive monkeys has been conducted, where their hair was analysed before and after the translocation and compared with respect to cortisol levels. The results showed that hair cortisol increased after the translocation, as predicted (Davenport *et al.*, 2006).

In my case, I specifically asked hunters to report the demographic group of moose (male, female, calf), partly because young individuals are expected to

have higher cortisol levels due to their heightened metabolism during active growth (Macbeth *et al.*, 2012). More importantly, I collected information about whether moose were health deprived or had injuries that hunters deemed were long term. I hypothesized that injured or otherwise health-deprived individuals would have higher cortisol levels in their hair due to increased amount of stress. As expected, I found that calves had higher cortisol levels than both males and females and that injured moose had higher levels than moose in healthy conditions (Paper III). That said, there are many questions that still need answers about the incorporation of cortisol into hair and the potential factors that may affect this physiological process.

3 Results and discussion

3.1 Antipredator behavior and cascading effects (Paper I and II)

Prey species responded to the variation in risk, both in the experiment (Paper I) and in my observational study (Paper II). Both studies suggest that horizontal cover is an important mediator of risk; closed areas appeared to be perceived riskier, as they had fewer ungulate visits (Figure 2) and lower probability of browsing than open habitats in areas where perceived risk generally was higher (areas with bear pelt or increased bear habitat selection).

Thus, ungulates may feel relatively safe while foraging in open forest stands, even in areas where brown bear use is generally high, because they have a greater chance to detect and escape an approaching bear. The fact that antipredator responses were present in the study area that were located outside brown bear range indicates that ungulate species perceived brown bear scent as a risk cue, even though they most likely never had encountered brown bear scent during their lifetime.

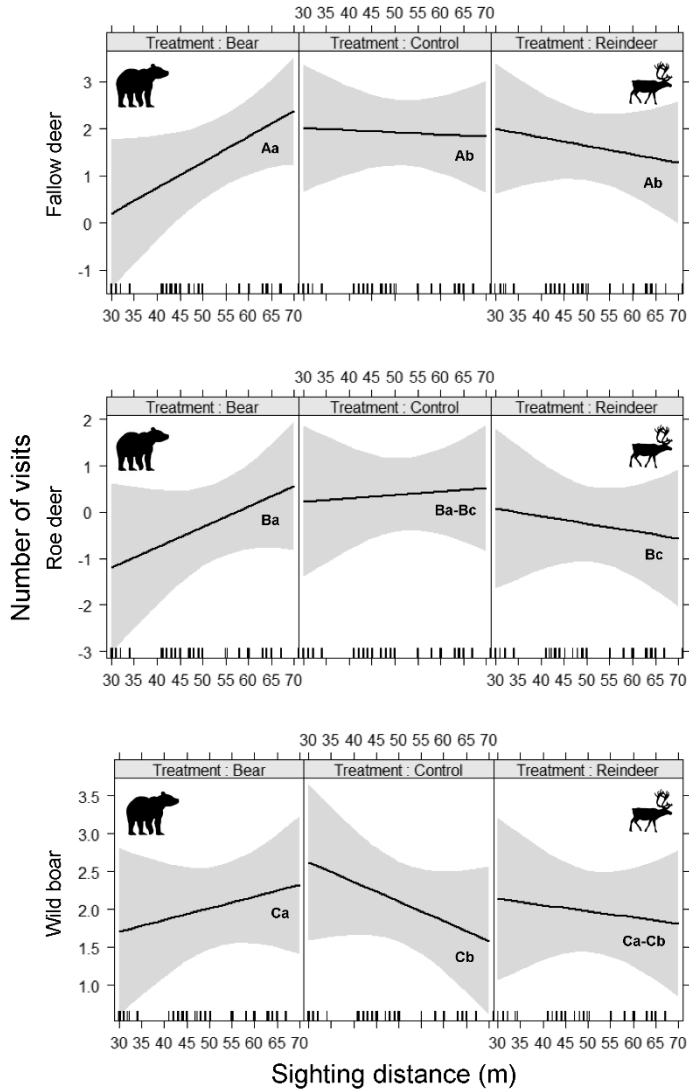


Figure 2. Model estimates of the number of weekly visits and sighting distance (habitat openness) for the three different treatments; brown bear scent (left), no scent (middle), and reindeer scent (right), for fallow deer, roe deer, and wild boar, in southeastern Sweden, March and April 2013. The grey zones represent confidence intervals and the letter coding below the slopes show significance between slopes (e.g., Ba is significantly different to Bc but not to another Ba or Ba-Bc).

Predators have the potential to induce trophic cascades and release plants from retarded growth by reducing browsing pressure (Hebblewhite *et al.*, 2005). Overall, my results show that the tallest sapling in the plot was taller in the more open areas, but the opposite was found where brown bear risk was high (Figure 3), which indicates that risk posed by brown bears has the potential to cascade across trophic levels and impact tree recruitment. In addition, the browsing height selection ratios showed that moose browsed at lower tree heights in areas with higher risk (Figure 4). This means that the risk of being browsed for a plant individual at a certain height is affected by predators; trees may reach safe heights, and escape browse traps, sooner when predators are present. Thus, my data demonstrate the presence of a three-dimensional landscape of fear that predators may evoke in browsers—a concept I introduce in more detail in Paper II.

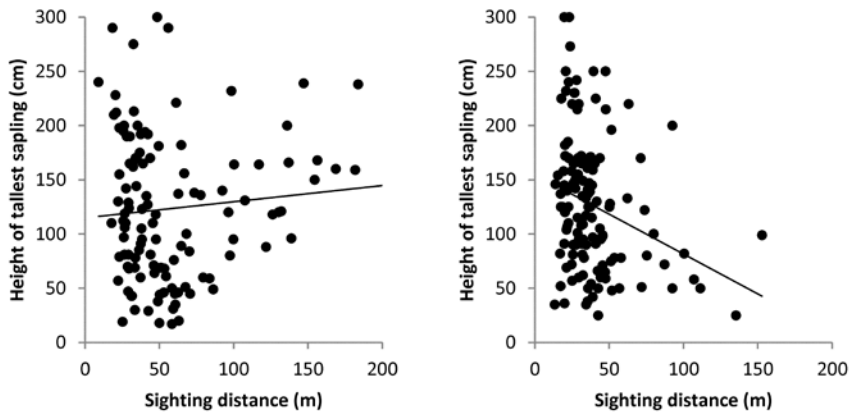


Figure 3. Relationship between the height of the tallest sapling in the plot, intensity of brown bear use (divided into low [left] and high [right] for graphics), and sighting distance in central Sweden, summer 2013.

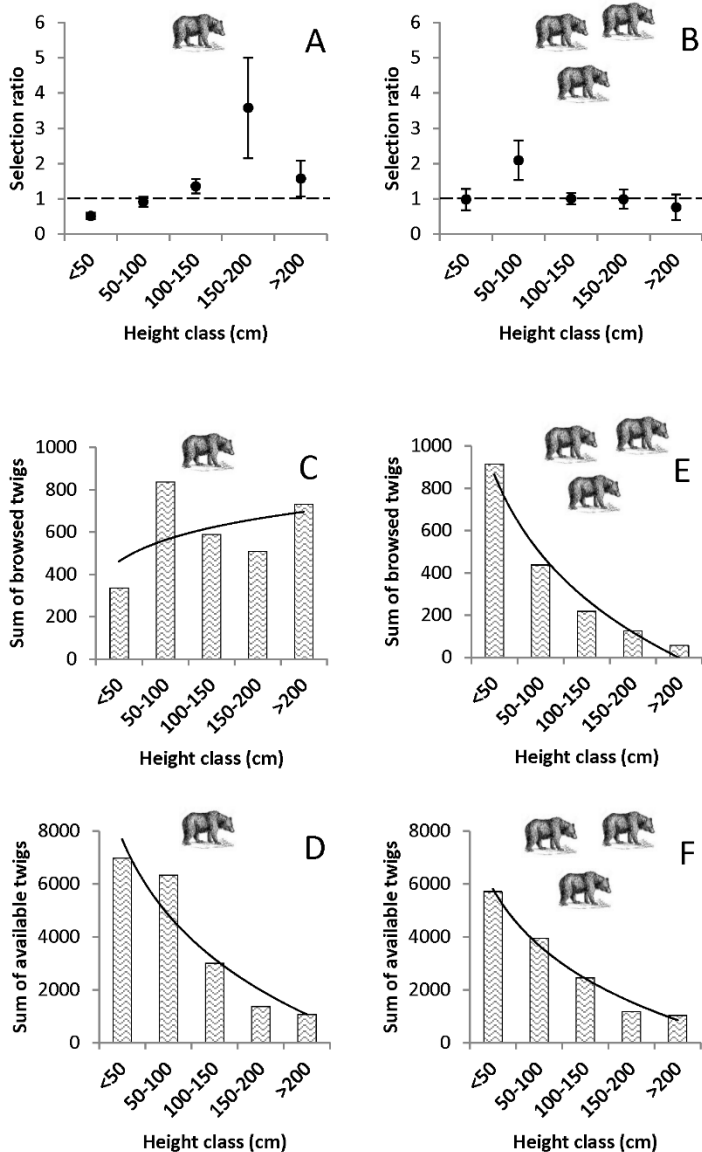


Figure 4. Selection ratios (proportion browsed / proportion available twigs) (A and B), total number of browsed twigs (C and D), and the availability of twigs (E and F), for areas with different intensity of brown bear use (divided into low [left] and high [right] for graphics) in central Sweden, summer 2013.

3.2 Hair cortisol levels in prey (Paper III)

I found that the most important variable in our analysis explaining the variation in hair cortisol levels in moose was the long-term average temperature sum (climate) in the area they lived. Moose in warmer regions generally had higher hair cortisol levels than moose in northern ranges (Figure 5). Being a ruminant adapted to colder climates moose are especially sensitive to warm temperatures (Renecker & Hudson, 1986) and when temperatures rise, moose increase activities that cool their bodies and decrease movement and food intake (van Beest *et al.*, 2012). In addition, parasitic load is higher in warmer regions (Malmsten 2014). Thus, a warmer climate may be negative for moose health for more reasons than the temperature increase per se.

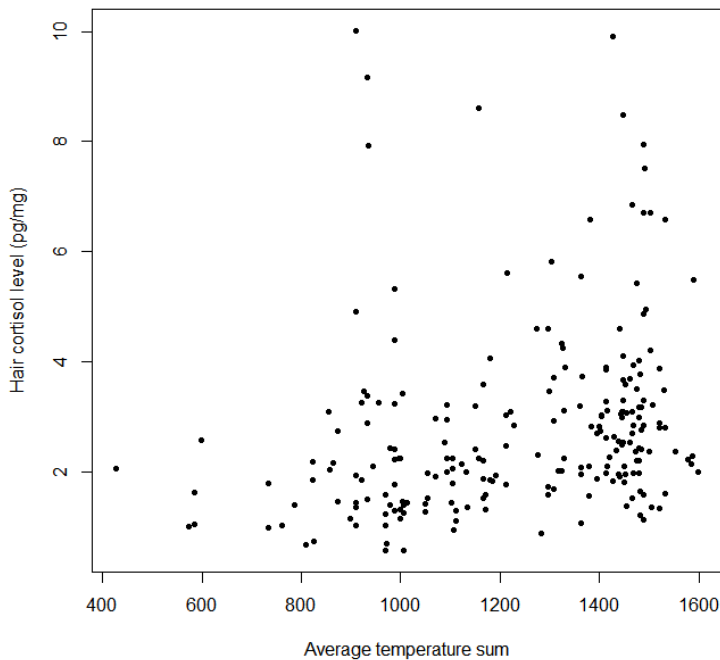


Figure 5. Moose hair cortisol levels in relation to the long-term average temperature sum in the area where they lived.

Higher hair cortisol levels were also associated with higher road densities; and the closer to towns and cities the moose lived, the stronger effect of roads on increasing cortisol levels. In other words, negative impacts of roads are stronger in areas where humans are more abundant, potentially due to a crowding effect or more human activity along the roads in those areas. Unexpectedly, large carnivore occurrence was associated with lower levels of hair cortisol in moose, indicative of a lower stress load in areas where large carnivores exist. I suggest this result may be due to lower levels of human disturbance in areas extensively used by large carnivores, a pattern supported by my data (data not shown). An alternative explanation is that the reduced competition for resources between ungulates in areas with high carnivore densities leads to lower stress levels.

3.3 Ecological effects of large carnivores and implications of their recovery (Paper IV and V)

Humans affect the ecological effects of large carnivores in most or all stages of the food web, and in areas with human activities ecological effects of large carnivores may not be expressed fully. In areas where large carnivores have been absent for a long time, consideration should be given to the fact that prey and people may have become inexperienced with predators, which could impact prey species negatively and generate massive human-wildlife conflicts upon the return of large carnivores.

4 General discussion and implications for conservation

In this brown bear-ungulate system, the carnivore affected prey distribution, prey foraging behavior, and lower trophic levels. Prey avoidance of brown bears and denser habitats may lead to increased contrasting risks with humans, as human activity commonly is higher in more open areas. Thus, prey may be pushed towards human activity areas in regions with large carnivores--with large carnivores occupying habitats in areas farther away from humans (Berger, 2007). In that sense, ungulates choose between ‘the lesser of two evils’, with higher stress levels and increased risk of human-caused mortality in those areas dominated by humans. As a result, in anthropogenic regions, humans may greatly impact predator-prey interactions by modifying landscape structure and habitat openness.

The idea of top-down trophic cascades by carnivores has in recent years been both attractive and increasingly controversial (Mech, 2012), especially in terrestrial ecosystems on the North American continent, where most studies have been conducted to date (Berger *et al.*, 2001a). Consequently, existing knowledge about top-down trophic cascades is biased toward North American national parks, and more studies are needed to understand how the existing knowledge is applicable to other systems. My data offer support for potential cascading effects of large carnivores on vegetation, at least in this system. However, because the study system is greatly affected by forestry and habitat fragmentation, the long-term effects are most likely weak and overridden by human impacts. The majority of forests in this region are dominated by disruptive ground preparation and clearcutting every 80 years or so (Kuuluvainen *et al.*, 2012). Thus, with regular intervals, humans dilute traces of cascading effects in areas where these could potentially have an effect, and thereby erase the long-lasting impacts that large carnivores could have in such systems.

Further, my results indicate that prey have retained antipredator responses to large carnivore cues, because they avoided areas that are perceived more risky. If a trait has been driven to fixation in a population due to strong directional selection in the past, it is likely to be retained for generations even without an ongoing selection pressure on that trait (Merila & Sheldon, 1999). This may explain why ungulates in my study area outside brown bear range still responded to brown bear scent. Predator avoidance by prey species without prior experience to the predator is important, because innate antipredator responses will likely reduce the risk of prey populations suffer from high predation rates due to naivety should predators return (Berger *et al.*, 2001b). However, in all its complexity, naivety likely emerges (and fades) along a continuum, and should therefore not be described as an all or nothing, black or white state (Carthey & Banks, 2014). Current research does not elucidate under which circumstances naivety evolves or persists in a population, but I consider it very likely that humans influence the naivety process for prey species in human-modified areas (Ericsson *et al.*, 2015), especially for those species extensively harvested by humans. Even in situations where species have experienced only short windows of natural selection without the presence of carnivores, prey may experience higher predation rates at large carnivore recolonization fronts due to the lack of a proper antipredator behavior; although, the naivety is suggested to fade within a couple of generations (Berger *et al.*, 2001b).

Importantly, the outcome of the first phases of large carnivore recovery in areas where humans dwell may be detrimental to the continuing existence of large carnivores, where a ‘first impression’ may last and cause persistent negative attitudes towards recolonizing carnivores. Similarly, inexperience of predators by humans should be incorporated into management along large carnivore recolonization fronts, as it may bring direct negative costs for humans that have adjusted to a life without large carnivores. Thus, interactions between prey, predators and humans are complex, interconnected, and highly context dependent, where humans have the power to greatly influence the behavior of both prey and predators, and thus determine the outcome of large carnivore recovery—especially so in human-modified landscapes.

It is increasingly clear that one of the overall greatest threats to future ecosystems and the wildlife they harbor is globally warming temperatures (McCarty, 2001), not the least in northern regions. In my study where I investigated hair stress hormone levels in moose, a species in many aspects adapted to cold climates, the most important explanatory variable was the average temperature sum in the area where the moose lived, a variable describing how warm the growing season generally is. Notably, these

temperature measurements were more important than all human variables (such as roads, human density, and towns) and the occurrence of large carnivores, which may indicate that globally increasing temperatures have the potential to negatively impact moose. The result that hair cortisol levels were lower in areas with large carnivores may reflect the lower amount of human disturbance in these areas; however, it is also possible that the more health-deprived individuals with higher stress levels are continuously removed by predation in these areas, leading to lower average levels. Yet, the absolute importance of warm temperatures, large carnivores, and other variables on moose hair cortisol levels, growth rates, and overall health awaits further investigation.

The essential strategy to conserve species—and in this case their interactions—is to save their habitats, and in our boreal systems that means forests. But not any forests. Seen from a global warming perspective, even-aged single-species forests are likely poorer at buffering temperatures compared to old-growth forests (Frey *et al.*, 2016), and especially so if the former are fragmented with roads and clearcuts. In addition, areas with forests that are not extensively used by the forest industry likely have lower human activity and fewer roads, which decrease the impact of human disturbances on predator-prey interactions. In addition to the growing amount of research pointing at great losses of biodiversity in even-aged monoculture forest plantations, this should call for more areas of old-growth forests set aside for conservation purposes. Finally, such conservation actions, may help restore the role of large carnivores at the apex position of ecosystems, with cascading effects on lower trophic levels at magnitudes more closely resembling those that once were.

5 Conclusions

Based on this work I conclude that:

- Ungulates in my studies avoided areas with associated with higher risk, and used the variation in habitat openness or terrain to decrease risk in the landscape, independent of previous experience with predators. Therefore, in anthropogenic landscapes humans may greatly impact predator-prey interactions by modifying landscapes and habitat openness.
- The effects of large carnivores in industrial forests may cascade and impact tree recruitment; however, such ecological impacts are most likely erased by current forest practices that reset any naturally emerging forest structure by clearing and clearcutting regularly.
- Warmer temperatures and human activities were associated with increased hair cortisol (stress hormone) levels in moose, which may have implications with respect to the globally rising temperatures. Moose generally had lower hair cortisol levels in areas with higher large carnivore densities, presumably as an indirect effect of lower levels of human disturbance in those areas.
- In anthropogenic regions, the ecosystem impact of large carnivores may not be expressed to the same extent, or in the same way as in more natural systems. In areas where predators have been absent for a long time, consideration should be given to the fact that prey and people may have become inexperienced with large carnivores, which requires proactive conservation efforts in areas where large carnivores are predicted to return.

6 Perspectives for future research

Many interesting questions were answered during the course of my PhD, but even more questions were revealed in the process (some of which may even be important...).

- The relative impact of direct versus indirect effects of predation on population growth is important to determine, partly because large carnivores' effects on prey species will not necessarily be related to large carnivore population sizes. In human-modified landscapes knowledge about these issues are especially important because predators are generally held at low numbers due to conflicts with humans. So, is the mere presence of large carnivores more important than their numbers when it comes to effects on prey population growth rates? We have limited knowledge about these issues, and especially so in human-modified landscapes. Meta-analyses have found that indirect effects often rival the effect of consumptive effects on prey populations (Preisser *et al.*, 2005). Therefore, the exclusive focus on consumption of most predator-prey models can be misleading for managers. Studies on these issues are currently conducted in elk-wolf systems in North America; however, little or no effort has been made in Europe so far. A better framework to quantify the limiting impact of indirect effects of predation will not only help managers predict impacts of predator removal and restoration on prey species, but also make it possible to apply this framework to quantify indirect effects generated by human activities.
- Further, if indirect effects are low (as for example in the starting phase of large carnivore recovery where prey species potentially are naive), the impact on vegetation are more or less only due to density-mediated effects (by the killing of prey individuals). As naivety passes, prey dynamics may

be driven by the mere presence of predators to a larger extent, and impacts on vegetation are instead trait mediated (because of changes in prey behavior due to risk). These two different cascades may impact vegetation differently, as one is driven by the landscape of fear, and the other by a large-scale reduction in overall browsing pressure and thus less specific. The European human-modified setting with all its gradients in predator and prey numbers offer outstanding opportunities to investigate these issues further.

- Due to the fact that human forest practices may swamp the cascading effects of large carnivores in forested systems due to stand-replacing forest harvests in regular intervals, studies should investigate the potential for large carnivores to impact lower trophic levels through cascading effects depending on harvest regimes in certain regions.

7 Sammanfattning (in Swedish)

Stora rovdjur har ofta stor inverkan på sina bytesdjur vilket kan leda till kaskadeffekter på hela ekosystem. I områden där människor lever, särskilt i rurala miljöer där jakt och boskapsskötsel är utbredda aktiviteter, hamnar stora rovdjur ofta i konflikt med människan. På grund av detta har stora rovdjur blivit utrotade från många områden där de en gång fanns. I min avhandling undersöker jag interaktioner mellan människa, predator, och bytesdjur, och hur stora rovdjur och människan påverkar habitatval, beteende, och stressnivåer hos klövdjur i en region som påverkats avsevärt av mänskliga aktiviteter. Jag använder experiment och observationsstudier för att mäta beteende och stressnivåer hos bytesdjur i områden med och utan stora rovdjur. Jag sammanfattar även de generella effekterna av stora rovdjur i områden som människor påverkat och betydelsen av rovdjurens återkomst för bytesdjur och människor.

I mina studieområden så reagerade bytesdjuren på en förhöjd (upplevd) predationsrisk, även där rovdjur (brunbjörn *Ursus arctos*) varit frånvarande i över ett sekel. Bytesdjuren valde att använda sig av öppnare habitat i områden där de uppfattade predationsrisken som högre. Variationen i predationsrisk påverkade sannolikt även rekryteringen av nya träd.

Högre temperaturer och mänsklig störning var relaterade med högre stresshormonnivåer hos älg *Alces alces*, vilket kan få konsekvenser med tanke på den globala uppvärmningen och det faktum att mänskliga aktiviteter breder ut sig i många landskap i dag.

Människan kan kraftigt påverka klövdjur, predator-bytesdjurinteraktioner, och därigenom påföljande kaskader. Ett sätt att minska effekten av människan är att bevara gamla naturskogar, eftersom dessa tenderar att ha lägre mänsklig påverkan (färre vägar och begränsad mänsklig aktivitet). Naturskogar har dessutom ett svalare mikroklimat. En annan viktig aspekt är att lindra konflikterna mellan stora rovdjur och människor, eftersom människors

uppfattning av rovdjur kan vara den viktigaste faktorn för rovdjurens återkomst till områden där de en gång fanns.

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